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THE DEVELOPMENT OF THE THALLUS OF SPHAEROCARPOS DONNELLII AUST.

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The Germination of the Spore

Previous descriptions of the germination of the spore of Sphaerocarpos represent two conflicting views. One of these is held by Leitgeb and Goebel, the opposing one by Campbell. These are the only authors who have described spore germination in Sphaerocarpos. Leitgeb (9), the first to study this subject, identifies the method of spore germination with that typical for the Ricciaceae and Marchantiaceae. There is, according to him, a germ tube formed, consisting at first of a single cell, and later of several tiers of cells arranged in groups of four. The terminal quadrant of this structure forms the germinal disc, and one of its cells becomes the apical cell of the thallus. The latter grows out in a plane at right angles to the long axis of the germ tube. The apical cell is at first two-sided, cutting off two sets of lateral segments; it is later replaced by a four-sided apical cell, forming dorsal and ventral segments in addition to the lateral ones, and thus causing the thickening of the thallus. The first rhizoid is formed very early, but he states that its connection with the sporeling was to him obscure, though obviously arising from a previous division of the original cell.

Campbell (3), studying spore germination in Riccia, was unable to confirm this account; according to him growth is continuous in one direction throughout the history of the sporeling, and there is no formation of a germinal disc or plate on the end of, and at right angles to, the germ tube. According to his description, the germ tube, consisting of several tiers of cells, is formed as described by Leitgeb, and from one of the terminal cells a two-sided apical cell, later replaced by a four-sided cell, is formed; but growth resulting from the segmentation of this apical cell takes place in the same direction as does that of the germ tube. He agrees with Leitgeb in classifying Sphaerocarpos with the typical Ricciaceae and Marchantiaceae so far as the method of spore germination is concerned, but differs from him in his description of the method by which this takes place. In his account of the process in Sphaerocarpos (2), he describes in detail the way in which the two-sided apical cell is replaced by a four-sided cell. The two-sided cell is divided by a basal (posterior) wall in a vertical transverse direction, and then begins to cut off three sets of segments instead of two, two lateral and one basal. Later, two sets of basal segments are formed, the one basal wall being replaced by two inclined to one another. Thus finally four sets of segments are formed, two lateral, one dorsal-posterior, and one ventral-posterior. He gives no details as to his method of studying this transformation. Campbell also states that the first rhizoid grows from the basal cell of the germ tube near the spore wall. It is not usually formed until the young plant is multicellular, and it is not separated from the germ tube by a wall. Later rhizoids arise from the older cells of the young thallus.

Goebel's description (7) in general confirms that of Leitgeb. According to him, however, it is impossible to say that the thallus develops from a single cell of the terminal quadrant of the germ tube, which cell functions as an apical cell from the beginning. On the contrary, all the cells of this germinal disc take part in the growth of the thallus, an apical cell is discernible only at a later stage, and one cannot determine from which cell of the germinal disc it was developed. He tends to bring together the two opposing views of Leitgeb and Campbell by calling attention to the fact that the formation of the germinal disc is not the development of a new structure from a sort of protonema, but is rather a simple flattening out of the young thallus presumably as a response to external conditions of air and light. The chief evidence in favor of this idea is found in a comparison with the method of growth in regeneration, which may resemble either description of the method of spore germination. He contrasts this type of development, which he calls "homoblastic," with that of the "heteroblastic" sort, in which the body of the plant arises secondarily from some sort of protonema.

A difference in species may perhaps account for the difference in descriptions. Campbell, according to Miss Haynes (8), was working with either (or both) *S. texanus* or *S. cristatus*. The European authors probably studied *S. Michelii* and *S. texanus*. It is also, of course, not inconceivable that differences in climate and in general habit might influence the course of development.

The description which follows is based on a study of sporelings of *S. Donnellii* grown from spores sown broadcast in a mixture of clay loam and sand and kept in a Wardian case in the greenhouse. When the young plants became visible under a hand lens as minute, bright green growths on the surface of the soil, they were picked up with a needle under a binocular microscope, the soil was washed off in water, and the plants were mounted in glycerin. A solution of chrom-acetic acid (chromic acid, 0.3 g.; glacial acetic acid, 0.7 cc.; distilled water, 99 cc.) proved most satisfactory for fixing. Various attempts were made to stain the sporelings, but without much success. They took the stain with difficulty and it did not prove permanent. However, since in most cases the cells were slightly plasmolyzed, the cell walls stood out fairly sharply although they did not always maintain exactly the original form of the cells.

Different attempts were made to germinate spores in culture solution, using that recommended by Marchal and Marchal (10), but it was impossible to keep the cultures free from fungi brought in on the spores or on small shreds of tissue. In some cases germination occurred, after about twice the normal period, and resulted in the production of some abnormal plants. I was unable to grow any of these plants to maturity, on account of the fungous growth which soon covered and choked them.

The spores sown in soil germinated usually about a month after sowing, in the case of those sown early in the spring. Some sown in early summer required three or four months to germinate. The first sign of germination is the appearance of a slender germ tube which pushes out through an irregular ruptured spot in the heavy spore wall. The spores from a greenhouse culture are at this time still united in tetrads, which is contrary to the usual description for *S. Donnellii* under natural conditions (8). The spores of a tetrad do not usually all germinate at the same time, and it is rare to find a tetrad with all four spores producing young plants. The germ tube is filled with dense cytoplasm, and contains from the first an abundance of chlorophyll, and there are often present in the early stages globular bodies having the appearance of oil droplets. As the tube grows in length, the dense contents become gathered at the distal end, leaving the basal end almost clear and quite colorless, and the first wall usually cuts off a terminal cell which contains all, or nearly all, of the dense cell contents. The length to which the germ tube may grow before the first cell division occurs varies considerably. This is evident from a comparison of figures 1 and 2, Plate IX. In cases in which I have made measurements, the length of the undivided germ tube varies from 0.3 to 1.6 mm. The majority of the germ tubes reach a length of about 0.5 mm. by the time of the first cell division. In the cases of the abnormal sporelings mentioned above which resulted from spores germinated in nutrient solution, the most remarkable feature was the great length to which the germ tube attained. It seemed to be able to grow indefinitely until the distal end reached the surface of the solution, at which time cell division usually occurred (fig. 35, Pl. X). Some that I have measured reached a length of 7 or 8 cm., and consisted of a single long hair-like cell with a small mass of dense green material in the extreme distal end, and only to be distinguished by this latter characteristic from the rhizoids produced at the same time.

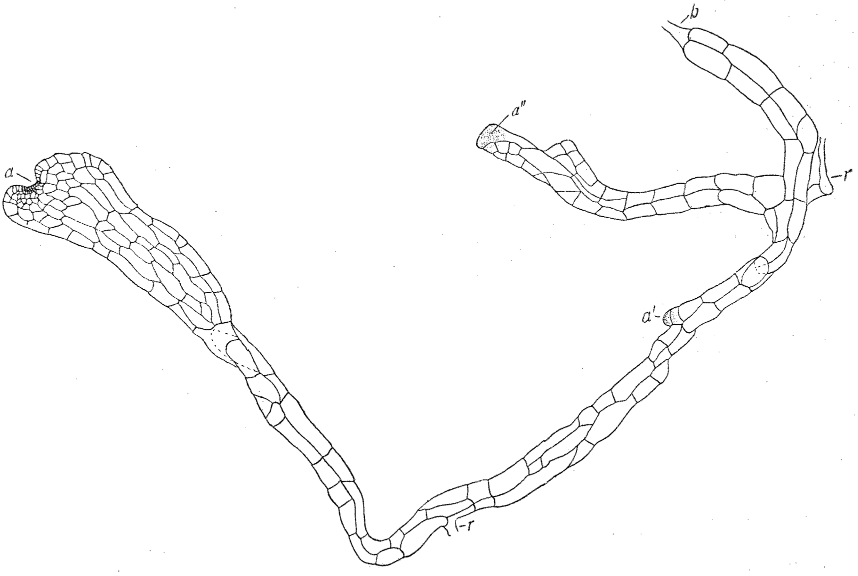
The first wall is transverse, and divides the germ tube into a large clear basal cell, from which only the first rhizoid develops and which undergoes no further division, and a small, densely-filled terminal cell from which the rest of the young thallus develops (fig. 2). The basal cell persists for some time, so that the young plant remains attached to the spore wall until well along in its development—until about the time when the secondary disc begins to be composed of two cell layers.

The second cell division occurs in a plane parallel to the first, cutting the terminal cell into two (fig. 3). About this time the first rhizoid usually appears, pushing out from the extreme base of the germ tube, and growing rapidly in the opposite direction. It is a simple slender structure, almost devoid of granular contents except at the extreme tip.

The next division is variable, and indeed the whole subsequent history, up to the time when the young thallus has been fully formed, is very inconstant. Figures 4 to 9 indicate some of the methods by which the development occurs. The end cell resulting from the second transverse division may divide longitudinally (fig. 4), or other transverse walls may first be put in, and any of the resulting cells may divide longitudinally (figs. 5, 7). The result is usually the same in all cases—namely, the formation of a small plate of cells (commonly six or eight) of about equal size arranged in pairs (figs. 6, 8). Occasionally, however, some of the longitudinal divisions may fail to occur, the result being a single cell at some point n the double row of cells in place of a pair of cells (figs. 7, 9, 11). The next divisions are also longitudinal, but at right angles to the preceding, the result being a series of several groups of four cells each, with, however, many departures from absolute regularity. Very frequently the groups consist of three cells instead of four. The arrangement of cells here is difficult to determine under the microscope, as dividing walls are often either in the plane of the slide or superimposed vertically one upon the other. Figures 13, 20, 21, and 23 represent the arrangement of the cells at this time. These figures are of older stages in the development of the thallus, but all the cells except those of the terminal group have remained undivided.

The cells of the end group now begin to divide, mostly by longitudinal walls, so that a plate of small cells is formed at the end of the germ tube (figs. 10–16). These divisions are apparently more rapid than those preceding, since the cells do not attain so large a size before redividing. The divisions seem to be quite irregular, and I failed to find any cell in these stages which could be recognized as an apical cell. In figures 10 and 12 there is shown a cell (*a*) cut off by a diagonal wall suggestive of the apical cell described for many liverworts; this appearance, however, is not the usual one. The typical appearance of the young thalli at this stage is best shown in figure 13. The groups of cells below the terminal plate undergo no further divisions, though rhizoids are often produced from them; the rest of the thallus develops entirely from the germinal disc. This disc is very conspicuous, though in certain views, when mounted and observed under the microscope, it is sometimes flattened out so as to suggest a flat plate growing in the same direction as that of the original tube (fig. 26), instead of being placed at right angles on the end of the latter. I have seen cases in which the direction of growth of the plate seemed really to be a continuation of that of the germ tube, but in all but one of these (fig. 24, Pl. XII) the sporeling had become separated from the spore wall, and hence could not be distinguished with certainty from the not infrequent cases of regeneration from small shreds of tissue in the soil. Regenerative shoots take on many different appearances, and often seem to grow for a time by means of a single two-sided apical cell, which is regularly wedge-shaped. The only resemblance to this condition that I have found in sporelings is in those grown in nutrient solution; in these instances the terminal cell seemed to function as an apical cell, forming a narrow ribbon composed of pairs of cells (figs. 35, 36, Pl. X), the whole gradually broadening out into a flat plate. In the latter stage, however, the appearance of an apical cell was lost, and lateral growing points often appeared, from each of which presumably, under favorable conditions, a thallus would have developed (fig. 37, Pl. XII; text fig. 1).

After the terminal disc has been formed, its further growth usually becomes markedly one-sided. This results from the development of a group of rapidly dividing initial cells at one side of the disc. This tendency is illustrated in figures 15, 17, etc., Plate IX. Division in this group of cells takes place in several planes all at right angles to the original divisions of the germ tube, so that a flat plate, one cell thick, grows out at right angles to the latter. At first the plate is cup-shaped, owing presumably to the more rapid growth of the edges; later, however, it spreads out into a flat blade. This process is illustrated in figures 17–26, Plates IX and XII. It is noteworthy that one of Campbell's figures (3) of a sporeling of Riccia bears a strong resemblance to some of these figures, such as figure 23. In most cases, growth occurs by the division of a few cells at one point on the margin of the plate. Sometimes two such groups of initials may be formed, resulting in a marginal growth of the thallus at two points (*a*, *a′*, figs. 27, Pl. XII, and 28, Pl. X). In the particular case shown in figure 27 there is



TEXT FIG. 1. An abnormal thallus which resulted from a spore germinated in nutrient solution: *a*, *a′*, *a″*, apical regions; *b*, basal cell; *r*, rhizoids. The cell walls at *a′* could not be seen on account of the density of the cell contents. Drawn from living material, × about 50. Compare figures 35 and 36, Plate X, and figure 37, Plate XII.

a cell at the apex of each lobe that has very much the appearance of an apical cell; but this is the exception rather than the rule. The typical group of initial cells is shown in figures 26 and 30–34 (Pls. IX, X). It consists of a marginal row of small cells of dense contents, rather longer than wide, all substantially alike as to size and shape. As these cells continue to divide, not enlarging to any extent, the segments cut off from them on the outside outstrip them in growth and form two lobes, one on each side of the apical region. This results in the formation of an apical notch, which may be median (figs. 26, 32, 33) or lateral (fig. 34). The lateral position of the apical notch is a common appearance; it is noted in the subsequent history of the plant in the formation of a small and a large lobe on opposite sides of the growing point, and frequently in the formation of short branches when the growing point forks.

After the young thallus has reached this stage in its development, it becomes more than one cell thick in the central portion. Just how this transformation is effected I have been unable to determine. Mounts *in toto* no longer prove satisfactory, owing to the density of the cell contents in the apical region; and the plants are still too small to be handled readily by ordinary methods of fixing and sectioning.

Apical Growth and the Formation of the Thallus Lobes

Both Campbell (2) and Leitgeb (9) describe the growth of the thallus as being due to a single apical cell which cuts off right and left lateral segments and dorsal and ventral segments. Campbell says that the lateral segments so resemble the apical cell in horizontal view that it is difficult to say with certainty that there is but one apical cell. Leitgeb describes the apical cell as lying at the deepest point of the notch in the forward margin of the thallus, and states that this notch is often so narrow that there is space only for a single small cell. He goes on to say, however, that sometimes the notch is broader, and more rarely it is quite wide, which appearance, he thinks, is a sign that forking is about to occur. The situation throughout, according to Leitgeb, is practically the same as that found in typical Ricciaceae and Marchantiaceae.

It is a difficult matter, in mature plants, to obtain sections passing through the growing point exactly in a longitudinal vertical direction, owing to the small size of the plant, and to the presence of a mass of involucres and lobes about the growing point. In many hundreds of slides, I have obtained two satisfactory series of sections of the growing point cut in this plane (figs. 38–54, Pls. X, XI), and some rather less satisfactory series cut in horizontal and in transverse vertical planes (figs. 55 67).

The plants which I studied were grown in a Wardian case in the greenhouse, and the shady conditions, the abundance of moisture, and the absence of any seasonal limitations of the growing period, were responsible for a more luxuriant growth of the thallus, with a corresponding increase in the size and number of the lobes, than is the case under natural conditions. The thallus, instead of being a simple small plate, the edges of which are cut into more or less crowded and overlapping lobes, as is the case in nature, took on the form of a central thick, distinct axis bearing leaf-like lobes irregularly on either side, and attaining a considerable size. The involucres also grew longer and were more cylindrical in form, the mouths often flaring out and becoming undulate. These peculiarities are even more noticeable if the plants are grown in petri dishes on filter paper moistened with a nutrient solution (fig. 70, Pl. XII). Campbell (2), working, according to Miss Haynes (8), on a mixture of *S. texanus* and *S. cristatus*, described similar forms occurring in nature under exceptional conditions of moisture and shade, but in these cases the production of sex organs was partly arrested, whereas in the plants I studied rather the reverse was true. The Douins (4, 6), studying *S. Michelii and S. texanus*, also mention the growth of abnormal plants under cultural conditions. According to the description of C. Douin (4), the plants usually possess in nature three large lobes with a mall "middle lobe" in each of the two apical notches. The figures of Allen (1), however, made from living plants grown under natural conditions, show a less schematic and more luxuriant growth.

Leitgeb (9) says that the lateral segments of the apical cell continue for a time to cut off dorsal and ventral segments in the same manner as the apical cell itself, but sooner or later a lobe cell is formed, which grows out by vertical divisions into one of the lobes. This is the same condition as is shown by longitudinal vertical sections through the apical region (figs. 38–54). In such a case it is extremely difficult to determine whether there is a group of apical cells present, or a single apical cell, which has formed new apical cells to either side in preparation for a forking of the growing region. My figures show several small cells, having the shape usually described for the four-sided type of apical cell, grouped together in the apical region (*a*, figs. 38–54); and, in the case of one of the apical regions illustrated, several such groups are present, each two consecutive groups separated by a young lobe (*l*, figs. 38–48). The presence of several groups of initial cells indicates presumably that the original group had divided several times in close succession, the intervals between the groups being occupied by lobe cells. This is usually the case under cultural conditions, and dichotomy is correspondingly rapid. An examination of the plants under a hand lens confirms this interpretation of the figures. The apical region is often very wide, and there are usually from one to four small lobes in it. The fact that each group of initial cells consists of cells all alike and all having the appearance of four-sided apical cells, seems rather to favor the idea that growth is not due to a single apical cell but to a group of initials. It may be, of course, that the condition depends upon the environment, and that in nature a single distinct apical cell exists, while in culture this single cell is multiplied without a corresponding forking of the growing region necessarily resulting.

The existence of a group of initial cells is similar to the condition in Marchantia as usually described. Mottier (11), however, inclines to the view that in Marchantia also only one apical cell is present.

In longitudinal vertical section these initial cells (*a*, figs. 38–54) are regularly wedge-shaped, cutting off narrow segments mostly, but not always, in alternate succession. Archegonial initials may be seen, as described by Leitgeb (9), Douin (5), and others, only one or two cells distant from the initial cell or cells, each apparently formed from an entire dorsal segment of the latter (*ar*, figs. 38–54). From the ventral segments mucilage hairs grow out, each consisting of a row of cells, the terminal cell being large, spherical, filled with dense contents, and provided with a large nucleus (*s*, figs. 38–54). In the preparations these mucilage hairs become more or less shrunken and torn.

Sections cut through the growing region in a horizontal and in a vertical transverse plane are less satisfactory than those just described, owing to the even greater difficulty of orienting the plants in the paraffin for this purpose. Figures 55–61, Plate XI, illustrate a series of horizontal sections, starting at the ventral side. The small cells marked *a* in figures 59 and 60 probably represent the apical group. They are noticeably more dense in content than any other cells in the sections, except those of the mucilage hairs. They are obviously dividing with considerably rapidity; and the varying length of the same cells in succeeding sections (*x*, figs. 59, 60) makes it probable that they are bounded posteriorly by an inclined wall, and therefore correspond to the initial cells shown in the vertical sections. The sections suffer from the fact that they are cut at a slight angle from the horizontal.

Figures 62–67, Plates X and XI, illustrate similar groups of cells as seen in vertical transverse section. The first series (figs. 62–64) is taken from a very young thallus, consisting of a simple plate one cell thick in all parts save in the center, where the cells are smaller, denser, and obviously embryonic. At the beginning of the series (fig. 62) there are two plates of cells, one cell thick, separated by an empty space—the apical notch—instead of by the group of initials. At one side in the drawings (*x*, figs. 63, 64) there are several large hyaline cells which disturb the otherwise symmetrical arrangement. This is probably due to a fold in the thin thallus-blade. Figures 65–67, Plate X, illustrate a similar series from a mature plant. Here also a group of similar embryonic cells (*a*) is present; but in this case they are cut slightly on a bias, so that at one side they seem to merge into a mature lobe (*l*), while at the other side there is no corresponding structure. It is unfortunate that none of the sections except those cut in the longitudinal vertical plane showed the young lobes so evident in the latter; unless the cells marked *y*, figures 57–60 (Pl. XI), may be interpreted as such.

A second method was used in order to determine the origin of the lateral lobes of the thallus. Single plants were isolated and grown in separate pots, and sketched each day under a binocular microscope. Young plants with only two or three lobes were selected in most cases, and watched in this way until they had attained the size of normal mature plants. The lobes differ sufficiently in shape and size so that one can feel certain that one is following the growth of each individual lobe from its beginning until maturity. The plants were kept in the Wardian case and showed the peculiarities of growth already described.

This study shows that the lobes of the thallus are formed at the tip and are pushed back into a lateral position, as they increase in size, by the elongation of the median portion of the thallus, or midrib. It is also seen that they are not "middle lobes" in the ordinary sense, that is, lobes produced simply by the outgrowth of the thallus between two divisions of the originally single growing region; for very commonly two lobes are formed at the same time, without any consequent branching of the thallus. If all the notches between the lobes represent divisions of the apical region, it must be that some of these branch regions are arrested in further development, and that their cells merely mature without dividing further. When one lobe is formed singly, it often resembles the ordinary "middle lobe" of such a form as *Ricciocarpus natans*, and the growth of the thallus continues on either side of the lobe. This, however, is not necessarily the case, since in many cases only one of the regions to either side of the lobe produces new growth, the middle lobe being pushed aside and coming to lie on one side of the central axis, without a corresponding lobe on the other side. This is of common occurrence, and is often responsible for the curving growth of the thallus as a whole.

In the light of the foregoing studies, therefore, it is reasonable to suppose that a lobe is formed by the occurrence of vertical divisions in a lateral segment of an initial cell, and this, as both the sections and the study of living plants show, may, at least in greenhouse cultures, occur anywhere in the apical region, irrespective of divisions of the latter.

In nature, the growth of the thallus, to judge from the accounts of previous authors, is apparently much like that of Riccia. According to Douin's (5) description of Sphaerocarpos, there are usually two notches, separated by a large middle lobe, present in a mature plant. In the notches are usually two other small lobes, with a growing point on either side—thus four growing points in all. At this point, he says, growth usually stops, though it is not uncommon to find plants having five large lobes with small ones in each notch. The growth, of course, is limited by the end of the growing season. The only difference between this history and that of Riccia, according to the same author, is the fact that in Sphaerocarpos the middle lobe remains undivided, whereas in Riccia it becomes cleft as the midrib elongates. Hence in the latter case the growth of the midrib is more rapid than the intercalary growth at the base of the lobes, while in the former case the reverse is true. In nature, evidently, the lateral segments of initial cells of the apical region merge together in their development to form the broad marginal wing of the thallus; while in culture the more rapid growth of the central portion of the thallus causes the separation of the tissue developed from each cell into separate lobes.

In the plants grown in culture, the involucres are often broadly open at the tip and show various irregularities in form. Dorsal lobes were observed in several cases, and there are gradations between these dorsal lobes and the normal involucres. The Douins (6) also mention these peculiarities. This suggests the idea that the formation of lobes and that of involucres may be intimately connected, and that the form of the entire plant may depend rather strictly upon the environment. One might go even farther and suggest that there is an evolutionary relationship between some of the higher lobed or leafy liverworts and the various forms assumed by the more primitive types. There is at least a close resemblance. In *Pellia epiphylla*, according to Douin (4), of two middle lobes produced by the forking of the growing point, one is arrested in growth, while the other continues its development, and then a new lobe appears in the notch between them, thrusting to one side the lobe which has ceased its growth. The lateral lobes of many liverworts may be formed in this way.

Plants grown under water by regeneration from involucres and from lobes cut off from the plant show the same abnormalities as those above described carried to an extreme, except that there is little or no branching and that sex organs are not abundant. The plant consists of a long almost cylindrical axis, bearing a few scattered and small leaf-like lobes.

The following is a detailed account of two of the plants studied as indicated above. They are typical of the history of all the other plants studied, so that it is needless to multiply examples.

Plant no. 1. Lobes *a*, *b*, *c*, *e*, and *f* (fig. 68 *A*, Pl. XII) have already reached maturity, and do not change their position in the subsequent history of the plant; they may increase slightly in size. Lobe *d* is an example of a "middle lobe," growing regions developing on either side of it. However, in the notch to the left of it, a single lobe forms (*g*, fig. 68 *B*), on only one side of which—between lobes *g* and *d*—is there any further growth. In the notch between these two lobes growth proceeds in the usual way. On the other side of *d*, at first only one lobe—*h*—is visible (fig. 68 *B*), but another—*i*—soon makes its appearance (fig. 68 *C*), and finally comes to equal *h* in size. This sort of thing is of common occurrence, and indeed the formation of these little lobes exhibits the greatest variability as to size, shape, number, and time of appearance. The further history of this plant illustrates how the lobes are pushed into a lateral position, while new lobes arise at the apical region. In the last sketch (fig. 68 *D*), lobes *h* and *i* are approaching their mature size, and two small lobes have made their appearance simultaneously between them. On the other side of lobe *d*, meanwhile, two lobes (*k* and *j*) have developed at the same time (fig. 68 *C*), and finally (fig. 68 *D*) are considerably spread apart and a single lobe is to be seen between them.

Plant no. 4. The two forward lobes, *a* and *b* (fig. 69 *A*), are spread apart until there is a wide notch between them and they occupy a lateral position (fig. 69 *B*). This notch is filled by a round mass of cells. Two new lobes, *c* and *d* (fig. 69 *C*), are formed simultaneously in this notch, at first being in a transverse and nearly vertical position. (In the drawing, these two lobes appear to be of dorsal origin. This is not actually the case, the illusion being due merely to the position in which the plant was seen when sketched.) These two lobes are then subjected to the same process of spreading, and a few days after (fig. 69 *D*) a new lobe, *e*, has appeared between them. Three days after this, this lobe has reached a considerable size, and there is a new small lobe on either side of it—lobes *f* and *g* (fig. 69 *E*). This occurrence of three lobes, not widely different in size, is also very common. In the last stage sketched (fig. 69 *F*), a single lobe—*h*—again appears on one side of this "middle lobe," and on the other side two small lobes, *i* and *j*, are formed at the same time. In the subsequent history of this plant, the formation of lobes went on in the same way, small lobes succeeding each other rapidly in a very various and complicated manner, with no apparent relation to the occurrence of branching except sometimes in cases where only a single lobe was formed at one time (*e.g.*, lobe *e*, fig. 69 *F*).

Branching always occurs by the division of the apical region. In nature it is limited by the short growing season of the plant, and the number of growing points found in plants living under natural conditions, as described by Douin, has been referred to above. In culture, however, the plants may live indefinitely, and profusion of branching is in keeping with the luxuriant habit of the plant as a whole under greenhouse conditions; and owing to the rapid elongation of the central axes of the branches, the latter are more easily distinguished from each other. By the gradual dying of the posterior part of the thallus, branching, under the conditions referred to, is an effective means of vegetative multiplication.

SUMMARY

1. The spore of *Sphaerocàrpos Donnellii* germinates by means of a slender filament of cells, the germ tube, on the end of which, and at right angles to it, is formed a germinal disc. The latter structure develops into the thallus of the mature plant.

2. The history of the formation of the germ tube is very variable.

3. The growth of the germinal disc does not seem to be due to the activity of a single apical cell, except in special cases. It is formed by divisions of all the terminal cells of the germ tube, and continues its growth through the activity of a group of cells on the margin which remain embryonic in character.

4. The apical growth of the mature thallus is due to a group of cells occupying the apical notch. These cells have the appearance of four-sided apical cells. The lateral segments which they cut off either resemble the mother cell, or go to the formation of the thallus lobes. The dorsal and ventral segments add to the thickness of the thallus in the median portion.

5. The marginal lobes of the thallus are formed by the division of lateral segments of the apical cells. Under natural conditions, successive lateral segments merge together in their development to produce a more or less continuous marginal wing. Under cultural conditions, the more rapid elongation of the median portion of the thallus causes the separation of the structures derived from individual lateral segments into distinct leaf-like lobes, attached laterally along a central midrib.

6. Branching of the thallus is due to a division of the apical group of cells into two such groups, a lobe occupying the region between. The formation of lobes is not necessarily related to branching.

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EXPLANATION OF PLATES IX–XII

All drawings, except figures 68, 69, and 70, were made with the aid of a camera lucida. In these cases the drawings were freehand sketches of plants as seen under a binocular microscope. Figures 25, 35, 36, 37, 68, 69, and 70 were made from living plants. Magnifications given are approximate.

FIG. 1. Undivided germ tube. × 150.

FIG. 2. First division of the germ tube: *sp*, spore wall. × 150.

FIG. 3. Second division of the germ tube. × 150.

FIG. 4. Third division of the germ tube: *sp*, spore wall; *r*, rhizoid. × 150.

Figures 1–4 are shaded to indicate the distribution of the dense cell contents.

FIGS. 5–9. Further divisions of the germ tube, prior to the formation of the germinal disc: *sp*, spore wall; *b*, basal cell. × 150.

FIG. 10. Beginning of the formation of the germinal disc: *a*, possible apical cell. × 350.

Fig. 11. Further divisions in the formation of the germinal disc: *b*, basal cell. × 150.

Fig. 12. The same: *a*, possible apical cell; *b*, basal cell. × 350.

Fig. 13. Two sporelings at the time of formation of the germinal disc: *sp t*, spore tetrad; *r*, rhizoid; *g*, germinal disc. × 50.

Fig. 14. Formation of the germinal disc (compare fig. 13, *g*). × 350.

Figs. 15–23. The young germinal disc. × 150.

Fig. 24. Young thallus continuing its growth in one plane, without formation of a germinal disc: *a*, possible apical cell; *sp*, spore wall. × 75.

Fig. 25. Germinal disc in a more advanced stage: *a*, apical region (the cell contents too dense to permit of the cell walls being distinguished); *b*, basal cell; *c*, place of attachment of the germinal disc to the germ tube. × 75.

Fig. 26. The initial cells at the apex of a young sporeling. × 150.

Fig. 27. Young thallus growing out in two directions, and possessing two apical regions: *a*, *a′*, apical regions; *c*, place of attachment of germinal disc to germ tube; *b*, basal cell. × 75.

Fig. 28. The apical regions of the plant shown in figure 27: *a*, *a′*, possible apical cells. × 150.

Fig. 29. The point of attachment of germinal disc to germ tube. × 150.

Fig. 30. Initial cells of a young sporeling. × 150.

Fig. 31. The same. × 350.

Figs. 32, 33. The same in slightly older sporelings, showing the formation of the apical notch. × 150.

Fig. 34. The formation of the apical notch in a lateral position. × 150.

Fig. 35. Abnormal sporeling from a spore germinated in nutrient solution. × 25.

Fig. 36. Detail of figure 35. × 150.

Fig. 37. Another abnormal thallus produced in the same way: *a*, apical region; *r*, rhizoid. × 75.

Figs. 38–48. Series of longitudinal vertical sections through the apical region of a mature plant: *a*, apical cells; *ar*, archegonia; *i*, involucres; *l*, lobes of the thallus; *s*, mucilage hairs. × 350.

Figs. 49–54. Another series of sections through the apical region of a mature plant, cut in the same direction as the preceding: *a*, apical cells; *ar*, archegonia; *ar in*, archegonial initials; *i*, involucres; *l*, lobes of the thallus; *s*, mucilage hairs. × 350.

Figs. 55–61. Series of horizontal sections through the apical region of a mature plant. Two sections omitted between figures 60 and 61. The first figure of the series is on the ventral surface of the apical region, the last one on the dorsal surface: *a*, apical cells; *ar*, archegonium; *ar in*, archegonial initial; *l*, lobe of the thallus; *s*, mucilage hairs; *x*, see text; *y*, possible lobe. × 400.

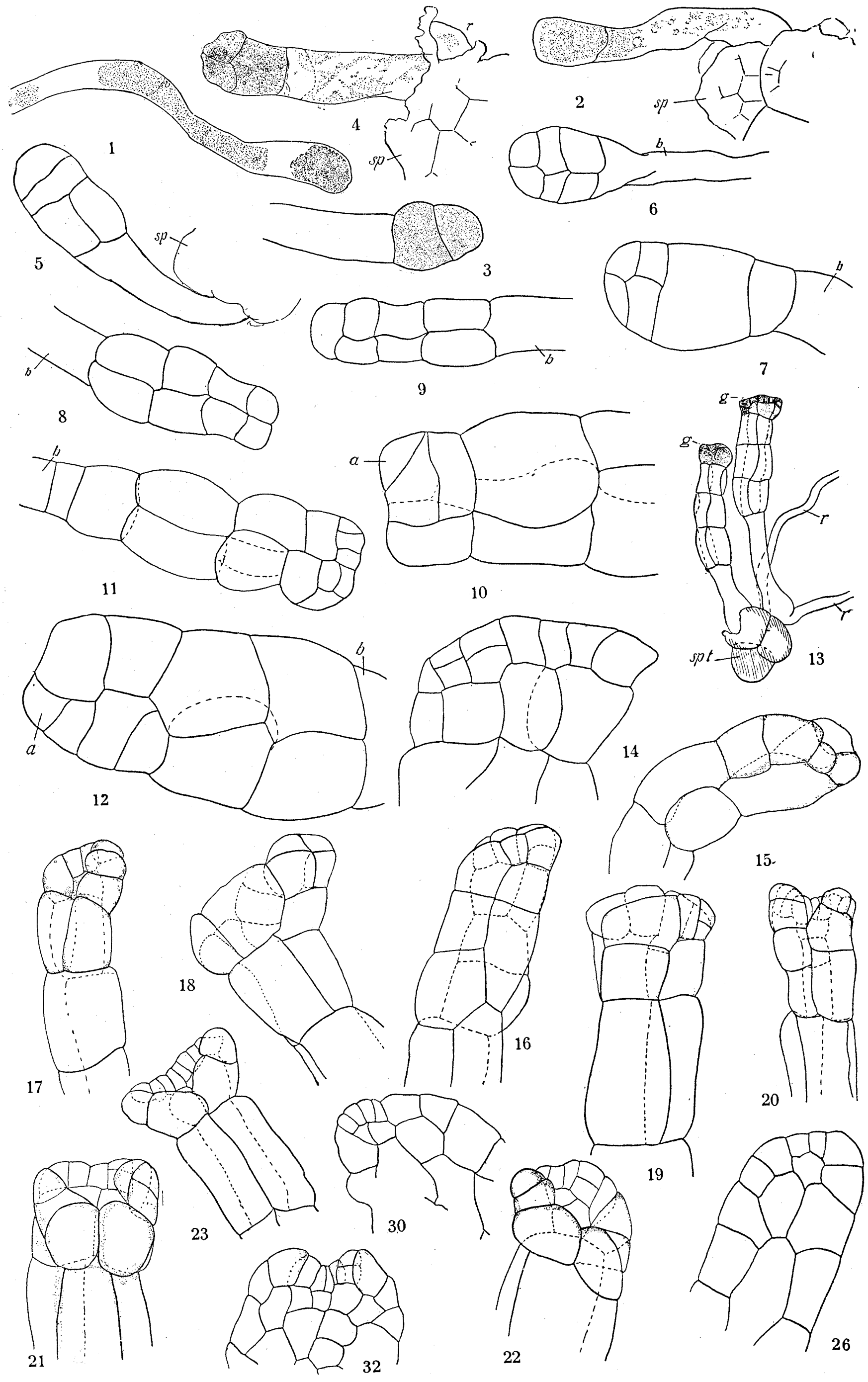
Figs. 62–64. Series of vertical transverse sections through the apical region of a young plant: *a*, apical cells; *s*, mucilage hair; *X*, see text. × 400.

Figs. 65–67. Series of sections through the apical region of a mature plant cut in the same way as the preceding series, but in a plane not quite perpendicular to the axis of growth: *a*, apical cells; *ar*, archegonia; *i*, involucres; *l*, lobe of the thallus; *s*, mucilage hairs. × 350.

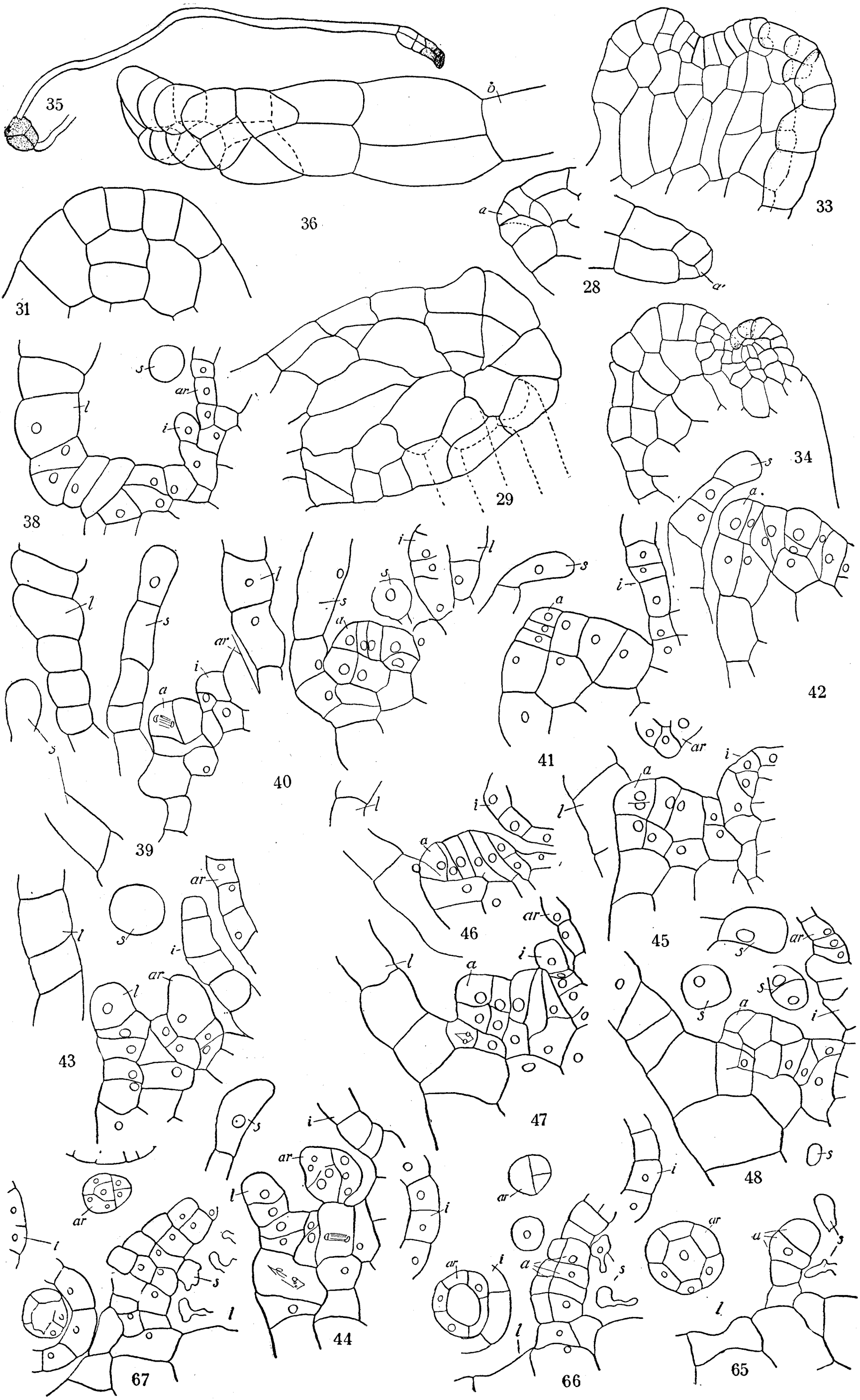
Figs. 68, 69. Two plants sketched at intervals of a few days in order to follow the origin and growth of the lobes of the thallus. Corresponding letters indicate corresponding lobes in each series. The following table shows the time which intervened between successive sketches.

Fig. 68*A*	March 8.	Fig. 69*A*	March 8.
Fig. 68*B*	" 13.	Fig. 69*B*	" 12.
Fig. 68*C*	" 16.	Fig. 69*C*	" 14.
Fig. 68*D*	" 19.	Fig. 69*D*	" 19.
		Fig. 69*E*	" 22.
		Fig. 69*F*	" 28.

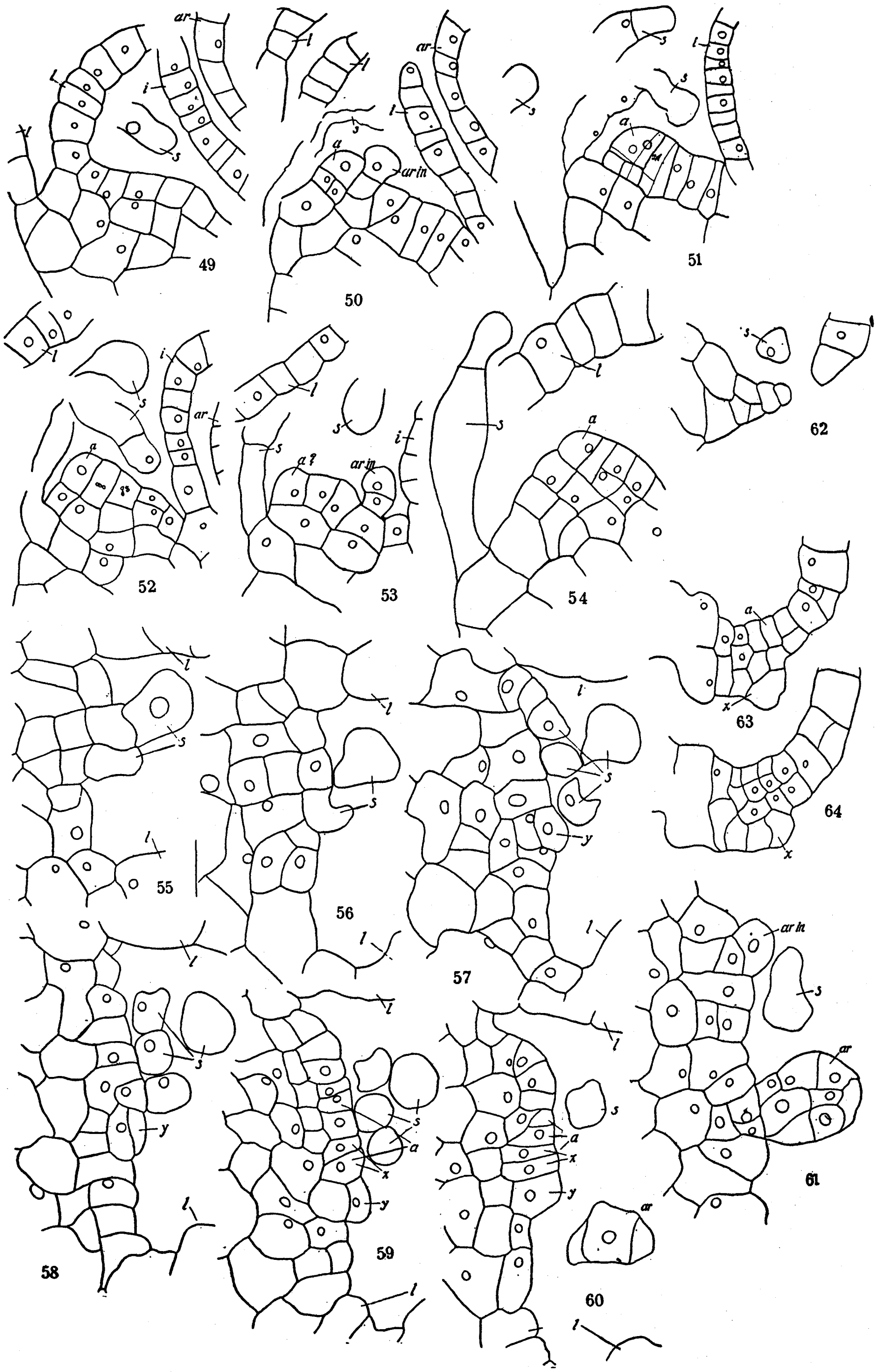
Fig. 70. Plant grown under conditions of excessive moisture, in a petri dish.



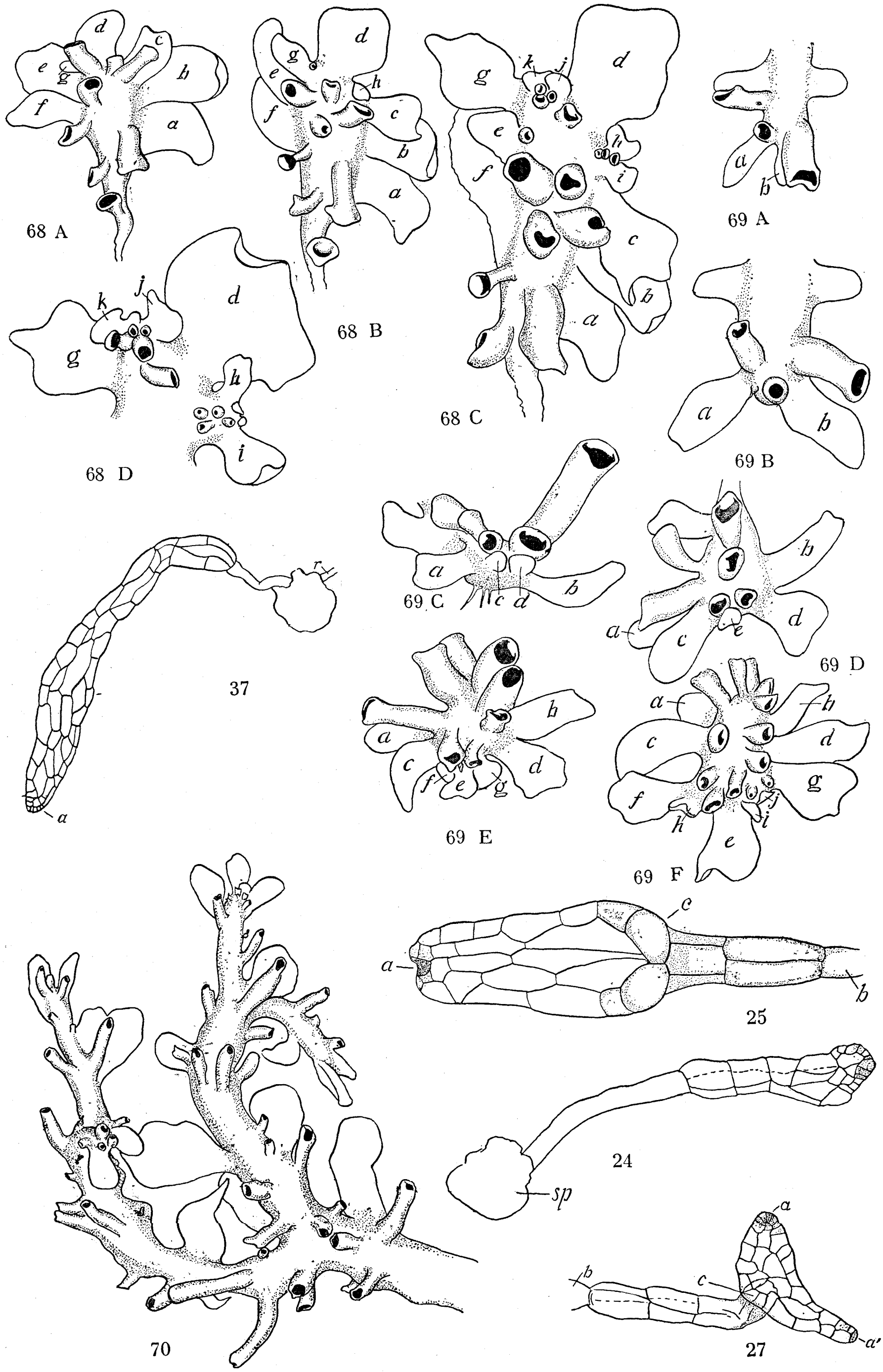
RICKETT: DEVELOPMENT OF SPHAEROCARPOS DONNELLII.



RICKETT: DEVELOPMENT OF SPHAEROCARPOS DONNELLII.



RICKETT: DEVELOPMENT OF SPHAEROCARPOS DONNELLII.



RICKETT: DEVELOPMENT OF SPHAEROCARPOS DONNELLII.